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Eternal enemies, or incidental encounters? Structure and patterns of interspecific killing in Carnivora

Tor G. Bertin

Virginia Commonwealth University

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by

Tor G. Bertin

B.S. Montana State University 2012

Major Advisor:

Dr. Salvatore Agosta, Department of Biology

Virginia Commonwealth University
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“*The lion does not turn around when a small dog barks.”*

-Kenyan proverb

Abstract:

Lethal interactions between carnivorans (interspecific killing) may influence their population dynamics, behavior, and other important aspects of their ecology. In this study, I expand upon previous research on the broad-scale patterns of interspecific killing in Carnivora (Palomares & Caro 1999, Donadio & Buskirk 2006) with a greatly expanded dataset (inclusion of scat and stomach data and more intensive sampling of the literature), and suggest avenues for future research. While like previous studies, I found a positive effect of relative body size between killer species and killed species on the likelihood of forming a killing interaction, I failed to find evidence that this effect had a body size ratio threshold above which interactions become less common, suggesting a greater role of non-competitive killing than previously believed. I also found evidence for a positive influence of range overlap and dietary overlap on species interactions, but found mixed effects of phylogeny. This study suggests that our previous understanding of the broad-scale dynamics interspecific killing in Carnivora was, due to limited sampling, incomplete in scope. Incidental killing, whereby killing interactions occur as a byproduct of opportunistic lethal encounters caused by the hyperpredatory behavior of carnivorans, has a number of interesting implications for our understanding of interspecies aggression, including research on intraguild predation and its effects.

Introduction:

Interactions between species are the core research focus of community ecology (Kordas et al. 2011). Ecologists have classified species interactions by whether each species is positively (+), negatively (-), or neutrally (0) impacted by the interaction (Dodds 1997). These interaction

types include mutualism (+/+, Boucher et al. 1982), commensalism (+/0, Heard 1994), amensalism (-/0, Osakabe et al. 2006), competition (-/-, Connor & Simberloff 1979), and predation / parasitism (+/-, Holling 1959). However, species interactions are dynamic, and can change in magnitude and character with different abiotic and biotic contexts. For example, Lee et al. (2009) found that branchiobdellid annelid cleaning of crayfish shells changed from commensalistic to mutualistic depending on surface fouling intensity. Similarly, the population-level impacts of species interactions, often those most relevant to wildlife conservation, may also change with predator or prey population density (Pech et al. 1982). Researchers have analyzed the broad-scale dynamics of species interactions in a diversity of taxa. For example, the influence of phylogeny on host-parasite interactions have been studied in parasites of seabirds (Paterson et al. 1993), primates (Cooper et al. 2012), fish (Sasal et al. 1999), and others.

Body size has been proposed to be an important component in many biological and ecological systems, including energy metabolism levels and associated lifespan (Peters & Peters 1986, Speakman 2005), biogeographic patterns (Meiri et al. 2005), ecological network structure (Woodward et al. 2005), foraging ranges (Greenleaf et al. 2007), and more. The influence of body size on interspecies interactions has also been studied in a great number of systems, including competitive interactions between ungulate species (Illius & Gordon 1992), foraging space use in Willow tits (Alatalo & Moreno 1987), and invertebrate predator-prey interactions (Warren & Lawton 1987, Brose et al. 2006).

However, despite their possible role as keystone species in terrestrial ecosystems, relatively little attention has been paid to interspecific interactions in Carnivora (Estes et al. 2011, Palomares & Caro 1999). Aggressive species interactions may play an important role in carnivoran community dynamics (Linnell & Strand 2000), which can in turn influence lower

trophic levels (Crooks & Soulé 1999). The most extreme form of aggressive interactions, interspecific killing (Lourenço et al. 2013), can affect carnivore behavior (Switalski 2003, Hunter et al. 2007), population ecology (Creel & Creel 1996, Helldin et al. 2006), and community ecology (Van Valkenburgh 2001). These effects may be either direct, through mortality or injury, or indirect, through changes in behavior to mediate perceived risk (Creel & Creel 2002).

Furthermore, through cascading effects, interspecific killing can affect lower trophic levels than those of the species forming a killing interaction (Estes et al. 2011). For example, Rogers & Caro (1998) found that song sparrow (*Melospiza melodia*) nesting success in the Lux Arbor Reserve of southwest Michigan was positively related to coyote (*Canis latrans*) abundance, and that predation rates on song sparrow nests were inversely related to coyote abundance due to mesopredator control. Similarly, Crooks & Soulé (1999) suggested that scrub bird diversity increased with coyote abundance in coastal California, mediated by both coyote predation on feral cats and changes in cat owner habits. Consequently, carnivoran interspecific killing may be an important influence on some ecosystems (Ritchie & Johnson 2009, Oliveira & Pereira 2014).

Because interspecific killing is the result of physical contests between organisms, body size can be a major factor in the outcome of aggressive interactions, with smaller species often falling victim to larger species (Palomares & Caro 1999, Donadio & Buskirk 2006). Grouping behaviors allow some carnivorans to offset body size constraints in interspecific conflict (Gittleman 1989), though multiple factors may have affected their evolution (e.g. increased hunting success and prey size access—Creel & Creel 1995). For example, African wild dogs and dholes are known to kill adult lions and tigers respectively (Schaller 1972, Turnbull-Kemp

1967), despite a large gap in median body size (victim species 7.2x and 10.8x the median body size of the killer species).

Researchers have proposed several reasons killings may occur between carnivoran species (Palomares & Caro 1999, Donadio & Buskirk 2006). Theory suggests that a superior interference competitor can coexist with or displace a superior resource competitor by engaging in aggressive interactions (Case & Gilpin 1974, Amarasekare 2002). Consequently, one carnivore species may kill another to reduce the intensity of exploitation competition (Case & Gilpin 1974—referred to as *competitive killing* in this paper). Secondly, a carnivore may kill another carnivore to reduce the risk of injury or death to itself or its offspring (Janssen et al. 2002). Finally, one carnivore may prey upon another, gaining nutritional benefits from the killing interaction (*predatory killing*). *Intraguild predation*, whereby a species kills and consumes a resource competitor, combines killing for competition with killing as predation (Arim & Marquet 2004). *Incidental killing* interactions are those in which the killer species does not compete with and does not feed on the killed species.

While written observations of killing interactions between carnivorans go back hundreds of years (for example, Vigne 1842 reporting on an Indian fox killed by a caracal), no authors had systematically reviewed carnivoran interspecific killing events until Palomares & Caro (1999). In their seminal paper, the authors described 97 pairwise species interactions formed by 27 different killer species and 54 different victim species. In a follow-up review, Donadio & Buskirk (2006) modified the dataset of Palomares & Caro (1999) by removal and addition of species pairs, for a dataset of 92 species pairs of 59 carnivoran species. Though not a global review, de Oliveira & Pereira (2014) examined the patterns of interspecific killing among South American carnivorans.

While de Oliveira & Pereira (2014) indicated that predatory (i.e. non-competitive) interactions were common, they were thought to be of relatively little importance by Donadio & Buskirk (2006), indicating that "available data … offer little support [of predation being an important component of interspecific killing]." To explain the paucity of predation, they suggested that killing interactions between species differing in body size by a factor of 5.4 or greater (a figure calculated from the data, and not theoretically derived *a priori*) are rare because there are no fitness benefits in killing an animal that is no longer a competitor.

However, the rarity of non-competitive killing relationships in the aforementioned reviews may be biased by their choice of data, and by limited sample sizes. Both Palomares & Caro (1999) and Donadio & Buskirk (2006) only examined carcass data in their reviews.

Because small species are likely to be underrepresented in carcass studies (e.g. interactions between jaguars and kinkajous—Rabinowitz & Nottingham 1986, Novak et al. 2005), neglecting dietary data may bias the reviewed literature in favor of larger killed species in interspecific killing interactions (Margalida et al. 2007). Mills & Mills (2016) found significant differences in cheetah dietary composition between incidental cheetah kills, kills of directly followed cheetahs, kills found through radio telemetry, and remains found in scats. Incidental carcass finds and radio tracked kills overrepresented large species like springbok, while smaller species (hares and springhares) were found in higher proportion in the kills of followed cheetahs and through scat analysis. These differences are likely due to the speed at which small carcasses are consumed and decompose. Relatedly, if large-bodied species are easier to locate at kill sites than small-bodied species, limited sampling of the literature may underrepresent interactions involving small-bodied species.

In this study I use a greatly expanded dataset (inclusion of dietary data and more intensive sampling of the literature) to examine the broad-scale patterns of interspecific killing in Carnivora, and suggest avenues for future research. In particular, I evaluate the evidence in relative support of the following hypotheses (see Table 1 for a summary):

1. *Competitive killing hypothesis.*

   The competitive killing hypothesis posits that carnivoran interspecific killing is predominantly performed to reduce the competitive influence of one species on another. Consequently, it predicts that species pairs with overlapping diets are more likely to form killing interactions than those without. It also predicts a peak body size ratio between killer species and killed species, above which interactions become less common due to greater differences in dietary ecology. Under the competitive killing framework, the energetic gains offered to the killer manifest through reduced competitive pressures, and not from eating the carcass.

2. *Predatory killing hypothesis*

   The predatory killing hypothesis suggests that carnivoran interspecific killing is largely a predatory phenomenon, where one carnivoran species consumes another to gain an energetic benefit. Unlike the competitive killing hypothesis, there should be no upper threshold of body size ratios between the killer species and killed species, particularly if carnivorans do not comprise the primary prey source of the killer species (making the proportionally smaller body size of the prey, therefore, less energetically limiting). Under

this hypothesis, the selective benefits gained by the killing event are through energy acquisition, and not through an alleviation of competitive pressure.

3. *Intraguild predation hypothesis*

The intraguild predation hypothesis combines the above two hypotheses: the killer species and the killed species must share a resource, and the killer species must consume the killed species for energetic gains. Because species separated by large differences in body size are less likely to overlap in diet, an upper threshold of body size differences above which killing interactions are less common should appear in the data if the intraguild predation hypothesis holds true.

4. *Incidental killing hypothesis*

The incidental killing hypothesis suggests that after accounting for the relative body size difference between the killer species and the killed species, interspecific killing in Carnivora is largely a byproduct of opportunistic lethal encounters caused by the hyperpredatory behavior of carnivorans. Under this framework, many killing interactions are selectively neutral, and emerge as a byproduct of behaviors that are positively selected for in other contexts (e.g. chasing and attacking a moving animal when energetic needs are otherwise filled). Like the hypotheses described above, it predicts that species of larger body size disproportionately kill animals of smaller body size. It does not predict an upper threshold of body sizes differences above which interactions become less common. The killer species may not feed on the killed species, even when they do not overlap in diet.

Methods:

DATA SET

To construct the dataset for the literature review, I searched Google Scholar for references reporting interspecific killing through dietary and/or carcass data for all citations published through late 2017. The search terms used included *Species name* AND diet, *Species name* AND "food habits", *Species name* AND "feeding habits", *Species name* AND predation, *Species name* AND mortality, and *Species name* AND "killed by." *Species name* denotes the common name and/or the binomial name for a species of carnivore. In cases where a species is known by multiple common names, I performed the same search terms for the most frequently used of those common names. I implemented these searches for all 245 terrestrial carnivoran species (Hunter 2011). Other references were located in the citations found in the Google Scholar search, and through citations described in Palomares & Caro (1999) and Donadio & Buskirk (2006).

For a reported interaction to be included in the dataset, the identity of both the killer species and the killed species must have been positively identified by the authors. From each reference, I recorded the common names of the species involved in a killing interaction, and the family of each species. In the observed mortality dataset, I noted whether the animals killed were juveniles, adults, or both. I also recorded ancillary data (number of scats, stomachs, collared animals, etc.) for both observed mortality and dietary datasets (see Supplementary File 1).

DATA ANALYSIS

I recorded species information, including median body mass values from provided mass ranges, taxonomic data, grouping behaviors, common names, and food habits from *Carnivores of the World* (Hunter 2011). Though I included interactions involving domestic cats and dogs within the dataset, they were excluded from quantitative analysis due to their artificially ubiquitous range and the difficulties in assigning meaningful body weights to the species.

Body mass measures:

To quantify body size differences between the killer species and the killed species in a killing interaction, I constructed the Body Mass Disparity Index (BMDI). The BMDI describes the relative difference in body size between two species in a killing interaction, and is bound between -1 and 1. BMDI values close to -1 indicate that the killer species is much smaller than the killed species, and values close to 1 indicate that the killer species is much larger than the killed species. Specifically, in those cases where the killer species is larger than the killed species, the BMDI can be calculated by:

$$\text{BMDI } M_{Killer} > M_{Killed} = \frac{M_{Killer} - M_{Killed}}{M_{Killer}}$$

Where M_{Killer} is the median body mass of the killer species, and M_{Killed} is the median body mass of the killed species.

However, though equation 1a has an upper bound of 1, it has no lower bound. Consequently, I modified the equation to calculate the BMDI for cases where the killer species is smaller than the killed species:

BMDI $M_{Killer} < M_{Killed} = -\frac{M_{Killed} - M_{Killer}}{M_{Killed}}$

Either equation can be used if the two interacting species are identical in median body size.

While the above equations create a simple and interpretable index, response variables bounded between -1 and 1 are not easily analyzed by regression models. Therefore, for statistical analyses (see below), I transformed the BMDI into a scaled index bounded between 0 and 1:

Scaled BMDI = $\frac{BMDI+1}{2}$

Competition measures:

To evaluate whether species with overlapping diet were more likely to form species interactions, I assigned each carnivore species to one or more dietary categories created by Caro & Stoner (2003). These included consumers of fruits and seeds, insects, fish, < 1 kg terrestrial vertebrates, 1-20 kg terrestrial vertebrates, and > 20 kg terrestrial vertebrates. If one or more of the above dietary categories were described as being common in a carnivore's diet in Hunter (2011), I assigned said dietary categories to the carnivore. Two carnivores in a species interaction were listed as being competitors if they overlapped in one or more dietary categories.

Therefore, ‘competition’ here is a broad measure, and sacrifices precision for large-scale applicability.

Species range overlap effects:

To determine the pool of possible species interactions, and to evaluate the influence of range overlap on the probability of two species forming a species interaction, I extracted the species range vector shapefiles provided by the International Union for Conservation of Nature in ArcGIS v. 10.1 for all non-domesticated carnivorans. Using the model builder feature to automate the process, I performed pairwise range intersections on all carnivoran species pairs, compiling a dataset of all species with overlapping ranges. I used the absolute area of range overlap between each species pair as a covariate in the examined models. Species range percentages, used to help data interpretation, were calculated as the percentage of the killer species’ range occupied by the killed species.

Phylogenetic distance

To evaluate the influence of phylogeny on the observed killing interactions, I calculated phylogenetic distance values between all species pairs by uploading the Carnivora supertree nexus file (Nyakatura & Bininda-Emonds 2012) into R v. 3.5 (R Core team 2018). Using the *ape* package (Paradis & Schliep 2018), I extracted the ‘best estimate’ supertree from the nexus file,

and constructed a matrix with the carnivoran phylogenetic distances, which were then added to the master dataset as a covariate.

Statistical methods:

I tested the effects of covariates on the probability of two species forming a killing interaction by fitting mixed effects logistic regression models with the observation (1) or non-observation (0) of each possible killing interaction (defined by two species having overlapping ranges) as a response variable. Examined fixed effects included the scaled Body Mass Disparity Index, the area of species range overlap, the phylogenetic distance between the two species, and the presence or absence of dietary overlap. Killer species, killed species, killer family, and killed family were included as possible random effects in the models.

Following the approach outlined by Zuur et al. (2009), I split the model selection process into two stages. First, keeping the fully parameterized fixed effects constant, I fit alternative combinations of the random effects, and calculated the AICc score for each (Burnham et al. 2011). The best fitting model (111 AICc over the next best model) had two random effects, one for killer species ID, and one for killed species ID, which I implemented into later model building stages. With the random effects structure chosen, I then evaluated the relative fit of a set of 16 different fixed effect formulations (all combinations of the four fixed effect covariates and one model with a fixed intercept). All models within a ΔAICc of 2 were determined to be the 'best models', for which parameter estimates were reported. To measure absolute model fit, I

recorded the marginal and conditional R^2 values estimated by the delta method (Nakagawa & Shielzeth 2012).

To calculate expected values for species interaction comparisons, I multiplied proportions of interest in the pool of possible interactions (e.g. the proportion of species pairs with overlapping diet) by the total number of species interactions observed in the data (430, excluding domestic species). For these purposes, continuous variables were placed into bins with 11 discreet intervals. When covariate sample sizes permitted, I used Yates' continuity corrected Chi-Squared Goodness of Fit tests to compare expected vs. observed species interaction counts (Haber 1980). Comparisons with categories of small sample size (expected value < 5) were performed with Fisher's exact tests (Mehta & Patel 1982). Mean values of continuous data were compared with continuity corrected Wilcox rank sum tests, which do not require the assumption of normality (Peto & Peto 1972). I quantified the relationship between killed species and killer species body mass by building simple linear regression models, with log predator body mass as the response variable and log prey body mass as an explanatory variable. To avoid the influence of scavenging on this estimate, I only incorporated the observed mortality data.

All regression models were built with the *lme4* package (Bates et al. 2015) in R v. 3.5 (R Core team 2018). AICc scores were calculated with the *AICcmodavg* package (Mazerolle 2017) and model R^2 values were calculated with the *MuMIn* package (Barton 2018). All other tests were performed in the base R package (R core team 2018).

Species interaction probabilities

To determine unobserved species interactions with high estimated probability of occurrence (a metric with possible conservation impacts), I fitted the model averaged logistic

regression parameters of the top models to the data, and extracted the predicted values in R. I then exponentiated the predictions to calculate the interaction odds ratios, which I transformed into probabilities by dividing the odds ratio of each species interaction by its odds ratio + 1 (Bland & Altman 2000). I then sorted these unobserved interactions by probability of observation and reported the 10 most likely with their associated probabilities.

Results:

Interactions summary

The literature review yielded 796 references describing 550 species interactions. Of these, 120 included domestic species, and were excluded from analysis, leaving 430 killing interactions between undomesticated carnivorans (see Figure 1). These represented 4.2% of all possible pairwise interactions between species with overlapping ranges. From this pool of 430 interactions, 196 were exclusively found in dietary data, 137 were exclusively found in carcass data, and 97 were found in both data types.

Felids were the most common killer family in both data sources, though they were proportionally higher represented in carcass data (61.5% of species interactions, N = 144) than in diet data (55.6% of species interactions, N = 163). Leopards (N=46), pumas (N = 39), and tigers (N = 21) were the most common felid killer species, while wildcats (N = 7), leopards, bobcats, and Canada lynx (all N = 6) were the most common felid killed species. Canids were the second most common killer family in the datasets, representing 20.9% of all killer species noted through carcass data (N = 49) and 30.7% of all killer species noted through scat and stomach data (N = 90). The most common canid killer species were gray wolves (N = 23), coyotes (N = 22), and

black-backed jackals (N = 16). Red foxes (N = 16) and bat-eared foxes (N = 8) were the most common canid killed species.

Smaller-bodied carnivoran families were proportionately higher represented as killed species in dietary than in carcass data (Figure 2). This difference was greatest for the Mustelidae, which were the killed species in 18.4% of interactions noted through carcass data (N = 43), and 27.3% (N = 80) of interactions noted through scat and stomach data. Mustelids were also the most common killed family overall, with 31 species killed in 105 unique interactions, followed by Canidae and Felidae (22 species killed in 91 and 64 killing interactions respectively).

Model rankings

The best performing random effects included random intercepts for the killer species and killed species (ΔAICc = 143.73—see Table 2). With the random effects included, the top model contained all covariates, while the second best model lacked the phylogenetic distance covariate (ΔAICc = 4.93—see Table 3). No other models fell within a ΔAICc of 5. Overall, the species-level random effects explained the most variation in the data (R^2_c = 0.64 for both top models), while the fixed effects explained less of the variation (R^2_m = 0.1 for both top models). Random effect variance was greater for killer species (SD = 2.8) than for killed species (SD = 1.6).

Body mass effects

The scaled body mass disparity index covariate showed a positive influence of relative body size on the probability of a species interaction in the dataset (model averaged $\beta = 3.29 \pm$

0.69). Differences between the observed and expected values of the full distribution of body mass disparity indices between interacting species fell short of statistical significance (Fisher's p ~ 0.08—see Figure 3a), but the tail ends of the distribution were markedly different from expectations. In particular, killing interactions with proportionally smaller killer species were underrepresented (killer species 0.2x the body size of killed species, Expected = 21.2%, Observed = 3.5%), while interactions with proportionally larger species were overrepresented (killer species > 5x the body size of killed species, 21.9% Expected vs. 51.2% Observed). In the observed mortality data, larger killed species were on average killed by larger killer species (β = 0.35, $p < 0.001$).

The killer species of the observed interactions were on average 2.5x the body size of the killed species (mean S_BMDI = 0.81, SD = 0.25), and separated by 5.5x the body size of the killed species at the median value. The modal peak (and majority, N = 229) of the observed species interactions were between killer species > 5x the body size of the killed species. The largest gap between killer species body mass and killed species body mass occurred between lions and yellow mongooses (M killer / M killed = 285). The slope of the linear regression equation between log killed species mass and log killer species mass was 0.35.

In 8 cases, species were able to kill species of larger body size by killing adult animals in packs (e.g. dholes killing tigers at < 10% their median body mass) or by killing the offspring of much larger species (e.g. black-backed jackals killing lion cubs and bobcats and coyotes killing black bear cubs).

Range overlap effects

The absolute area of species range overlap positively influenced the likelihood of two species engaging in killing interactions (model averaged β = 0.001 $\pm$ 0.00014, Fisher's p < 0.004—see Figure 3b).

Species pairs with ranges that overlapped by < 10% were markedly underrepresented relative to their frequency in the potential species interaction pool (Fisher's p < 0.01—Figure 3e). Species ranges overlapping by > 10% were greater than expected to in proportion with expectations. Species ranges between interacting species overlapped by an average of 39.55% (SD = 32.48%), and significantly differed from the 31.04% mean value (SD = 34.27%) of the range overlap pool (Wilcox rank sum test: p < 0.001). Ninety-four of the observed killing interactions were between species pairs with less than 10% overlap, and there were 13 species interactions between species pairs with < 1% range overlap. Most of these were between killed species of limited range and wide-ranging killer species (e.g. coyotes killing black-footed ferrets, red foxes killing kit foxes).

Diet overlap effects

Interactions with overlapping diet were less common than expected in the raw data (χ^2 = 26.61, df=1, p < 0.001—see Figure 3c). However, this effect does not appear in the models when species identity is accounted for (model averaged β = 1.23 $\pm$ 0.3). Felids killed more species with non-overlapping diet than expected by their proportion in the possible interactions, and fewer species of overlapping diet than expected (χ^2 = 53.01, df=1, p < 0.001—Figure 4a).

Dietary overleap for interactions with canid killer species, on the other hand, occurred in proportion to their occurrence in the range overlap pool (χ^2 = 0.02, df=1, p < 0.89—Figure 4b).

Phylogeny

The influence of phylogenetic distance between interacting species was mixed. Firstly, incorporating phylogenetic distance as a fixed effect had no discernable impact on the other parameter estimates of the model covariates (see Table 4), suggesting that the model conclusions are robust to interspecific correlations of ecology and body size. The estimated phylogenetic distance parameter, which appeared in the second-best model and was absent from the top model (β = 0.0025, $\pm$ 0.002—see Table 3 and 4) did not significantly differ from zero (z = 1.1, p > 0.26).

The overall distribution of the observed phylogenetic distances differed from expectations (Fisher's Exact Test: p < 0.001). An examination of the two distributions suggests that these differences were greatest at intermediate values of phylogenetic distance, with some deviation at high phylogenetic distance values (Figure 3e). Most of these intermediate values were between small-bodied, omnivorous feliforms (e.g. procyonids and mephitids), which rarely predate on medium-sized mammals. There was no evidence for a within-family phylogenetic influence on killing interaction frequency in the data.

The observed phylogenetic distance values and their relation to expectations varied by killer family and killed family. Phylogenetic distances of species killed by both felids and canids were proportionate to their availability (see Figure 6). Felids killed in the observed interactions were disproportionately killed by other felids, and correspondingly less frequently killed by other

carnivoran families (Fisher's Exact Test: $p < 0.001$—Figure 7). Canids and mustelids on the other hand, were killed in proportion to their availability. Herpestids were killed more often by other feliforms, including hyaenids and felids, than expected (Fisher's Exact Test: $p < 0.001$). Procyonids and viverrids were disproportionately killed by felids and canids relative to availability (Fisher's Exact Test: $p < 0.001$).

Interaction probabilities:

All overlapping species interactions with model estimated probabilities > 0.84 were observed in the dataset. Unobserved species interactions with estimated probabilities > 0.7 mostly comprised interactions between large-bodied killer species and small to medium killed species with high range overlap values. These included pumas killing crab-eating foxes, American martens, and margays ($p = 0.84$, 0.82, and 0.82 respectively), black-backed jackals killing wildcats ($p = 0.82$), and wolverines killing red foxes ($p = 0.82$). Observed species interactions with low observation probabilities included a clouded leopard killing a binturong ($p = 0.0027$), a small-spotted genet eating a least weasel ($p = 0.0058$), and a jaguarundi killing a Pampas fox ($p = 0.0087$).

Discussion:

The observed findings based on a greatly expanded dataset are in mixed, but broadly affirmative, support of previous research on carnivoran interspecific killing (Palomares & Caro 1999, Donadio & Buskirk 2006). As predicted by all hypotheses, interaction probabilities

increased with higher body mass disparity values, though contrary to the competitive killing hypothesis they did not decline above a certain threshold.

In the models, fixed effects had relatively low explanatory value (though above average for ecological research—Møller & Jennions 2002), while random effects comparatively captured a great deal of the model heterogeneity (though see Nakagawa & Shielzeth 2012 for a discussion on the somewhat nuanced interpretation of mixed effects models R^2). While the inclusion of both killer species and killed species random effects significantly improved model AICc scores (justifying their inclusion), the variance for the killer species effect was nearly three times larger than the variance of the killed species effect. This suggests that the identity of the killer species has a greater influence on determining whether a killing interaction forms than the identity of the killed species, which is consistent with predatory ecologies playing an important role in structuring interspecific killing (Donadio & Buskirk 2006—also see Phylogeny and Dietary Ecology sections below).

I address each of the proposed influences on interspecific killing in Carnivora below. I then examine what broad conclusions can be made from the analyzed data.

Body mass influences

As found in previous studies, body size appears to serve as an important constraint on carnivoran lethal interactions, with species interactions less common than expected at killer species to killed species body mass ratios below 2.5 : 1 (a somewhat higher value than the 2 : 1 ratio reported by Donadio & Buskirk 2006). Some interactions at the low end of the body mass

ratio were caused by probable scavenging events in the dietary data (for example, an American marten with bobcat remains in scat samples—Cumberland et al. 2001), by social species grouping together in aggressive conflict (e.g. dholes killing tigers—Turnbull-Kemp 1967), or by interspecific infanticide (e.g. black-backed jackals killing lion cubs, the lowest body size ratio in the dataset at 0.04:1—Hayward et al. 2007). Contrary to Donadio & Buskirk (2006)'s findings, I did not find that killing interactions became less common than expected above body mass ratios of 5:1. In fact, said ratios were the modal body size category in the data, and occurred over twice as often as expected. This discrepancy is likely influenced by an increase in sampling intensity of references reporting carcass data and by the inclusion of dietary data, which are more likely to capture small-bodied species (Mills & Mills 2016, Owen-Smith & Mills 2008, Tambling et al. 2012).

The relationship between log killed species weight and log killer species weight scaled remarkably similarly to those reported by meta-analytical studies of predator-prey ratios in both aquatic and terrestrial food webs (the estimated coefficient in this study, 0.35, was identical to that derived by Cohen et al. 1993). This is the first time that said coefficient has been calculated for carnivoran interspecific killing. It is interesting to note that the coefficient in Cohen et al. (1993) was derived from feeding networks, while those in this study included many killing interactions where the killed species was not fed on. This suggests that food web scaling coefficients may be at least in part driven by biophysical constraints unrelated to energy transfer content (Bertin in preparation).

Range overlap.

The positive effect of species range overlap on the probability of two species forming a killing interaction in the dataset is in line with my *a priori* expectations. Particularly, species pairs with less than 10% range overlap occurred half as frequently as expected in the dataset, while those greater than 10% occurred either more often than expected or in proportion to expectations (see Figure 3d). The absolute area of range overlap showed a similar pattern (Figure 3b)

While killed species occupying killer species ranges by < 10% did reduce the probability of an interaction in the dataset, it did not outright exclude it, and indeed was the modal category, at 94 interactions. It should be noted that the lack of interaction exclusion at low overlap values says nothing about the population-level impact or coevolutionary potential of species pairs engaged in interspecific killing. In a theoretical analysis, Nuismer et al. (2003) found that though host-parasite interactions could occur at small overlap values, there were range overlap thresholds above which would trigger a coevolutionary response to parasites in the host. These thresholds were contingent upon the explicit spatial configuration of parasite presence.

In this review, I do not examine the population-level or behavioral impact of interspecific killing, but it is plausible that those impacts are affected by range overlap extent.

Dietary ecology.

The data showed mixed support for the positive effect of dietary overlap on interspecific killing probabilities. Firstly, in the raw data (with killer species identity not accounted for in the

random effects), interactions of overlapping diet were less common than expected, while interactions with non-overlapping diet were more common. The negative effect in a model fitted to the raw data changed sign to a positive association with the inclusion of the killer species random effect. This is likely driven by several widespread, large-bodied predators, which are both heavily sampled across their range and overlap with many smaller-bodied carnivorans which do not feed on medium or large-sized animals (e.g. leopard, puma). For example, in the raw data, 85.5% of all species pairs have overlapping diets. The leopard, appearing as the most common killer species (N = 46 unique killing interactions), only overlapped in diet with 14.2% of possible species pairs.

The question of whether the positive effect of dietary overlap found by the best models is driven by a genuine propensity to engage in killing interactions with sympatric competitors as predicted by the competitive killing hypothesis is somewhat uncertain. Leopards and pumas, the most heavily sampled killer species, killed organisms of non-overlapping diet in proportion to their availability. Conversely, those with smaller sample sizes (e.g. lion, tiger, and jaguar) killed more species of overlapping diet than expected by their availability (see Supplementary Figure 1). It's noteworthy that lions, whose kills are more readily located and sampled than more cryptic felids, have very few studies examining diet through scats relative to kills (personal observation). This in turn may influence the underrepresentation of killing interactions with non-overlapping diet.

Phylogeny.

The data examined suggest a mixed role of phylogeny in structuring the killing interactions. Firstly, I found no evidence that the probability of a killing interaction changed with decreasing phylogenetic distance values within family. This runs contrary to the expectation that closely related species, which have highly correlated dietary habits, disproportionately engage in interspecific killing. As suggested by Donadio & Buskirk (2006), this may be because the increased rates of contact and resource competition of two closely related species are offset by their similarity in body size, which renders any given conflict more dangerous and so less likely to occur.

I found some evidence for family-level effects in the killing interaction patterns. Firstly, all of the families with more than 10 interactions as the killer species did not bias their killing patterns in favor of particular phylogenetic distances. This suggests that once a family is sufficiently predaceous, their targets are more constrained by body size limitations than any overlapping ecologies. Conversely, several killed families were killed disproportionately by species at certain phylogenetic distances. Herpestids, procyonids, and viverrids were all disproportionately killed by felids, and less frequently killed by canids. Felids, most strikingly, are most often killed by other felids, at levels 2-3x more often than expected. Conversely, they are killed approximately half as often by other families as expected. This is likely because felids more than other carnivoran families are equipped with large body sizes and hyperpredatory lifestyles (Christiansen 2008).

Canids were just as likely to be killed by other canids as by felids, despite being closer in body size. This may suggest a stronger force of competitive interactions within Canidae (as with, for example, artic foxes and red foxes—Frafjord et al. 1989, Tannerfeldt et al. 2002, Pamperin et al. 2006) than between Felidae and other carnivoran families. Despite this family-level

heterogeneity, both between-family killing interactions and within-family killing interactions occurred in proportion to their availability when all interactions were pooled.

Causal interpretation of interspecific killing

Though selection can operate on behavior, it does so through biophysical systems that are subject to multiple competing or synergistic influences (Hogan 2015, Krakauer et al. 2017, McGill 2019). For example, aggression between male lion coalitions may result in increased androgen concentrations (Fuxjager et al. 2010). These, in turn, modify the temperament of the affected lions, which renders them more susceptible to aggressive behaviors (Edwards 1969, Simon & Whalen 1986). These behaviors could have indirect effects on the lion's relation to other species: a jackal that walks by without conflict in one context could be killed when near the same lion after a fight (Briffa et al. 2015). In this hypothetical, the jackal was not killed for a competitive or predatory benefit, but because the neurology triggering intraspecific aggression was hijacked by a selectively neutral interspecific context.

Suggesting a greater understanding of animal behavior causality than can be justified by the available data may have consequences for broader ecosystem research, including studies of intraguild predation. A hyper-adaptationist view of killing interactions (one that ignores the role of incidental killing) restricts the pool of possible victims to those that offer energetic gains, through predation or through the alleviation of competitive forces (Lloyd 2015). Surplus killing, whereby carnivorans kill many more prey animals than can be consumed during the killer's handling time, has been reported for a great number of carnivorans, and is often thought to be environmentally driven (Kruuk 1972, Oksanen 1985). The incidental killing hypothesis proposed here offers an elaboration: predators may kill organisms that they have no intention of eating if

the energetic costs of doing so are not prohibitive (i.e. the behaviors are selectively neutral) and the same behaviors in other contexts are beneficial. Play behavior is a potentially adaptive source of killing unrelated to predation or competitive killing (Martin et al. 1985).

Summary and future research

Contrary to previous findings, which indicated that competition was the predominant driver of carnivoran interspecific killing (Palomares & Caro 1999, Donadio & Buskirk 2006), the data described here suggest that this picture is incomplete. While we can delineate killing interactions between species of overlapping diet vs. non-overlapping diet (and so determine a course measure of whether a killing interaction is 'competitive'), it is very difficult to assign causality to any given killing interaction. Papers frequently did not specify whether carcasses were fed on, though scat and stomach data come from interactions between both competitors and non-competitors. This made it difficult to separate competitive killing interactions from intraguild predation, and incidental killing interactions from predatory interactions through carcass data.

Instead, the data suggest a conceptual filter of 'killing potential', where whether a killing interaction occurs is largely a byproduct of the killer species being sufficiently large relative to the killed species and the killer species being sufficiently predaceous. The most common killer species in the dataset (leopards and pumas) are large, widespread, well-researched hyperpredatory carnivorans. There was no evidence that they avoided small-bodied organisms that lack competitive potential, and did not always eat said organisms when they killed them.

While there are undoubtedly selective pressures that influence the presence of interspecific killing, it's probable that those selective pressures can lead to neutral, non-adaptive killing interactions when the costs of engaging in the killing are low (Lahti et al. 2009).

The generally ignored frequency of incidental interspecific killing interactions suggests that the force of top-down influences on ecosystem dynamics may be stronger than would be assumed than if all killing interactions were inherently driven by food or competition, as the pool of possible victims is larger. It also indicates that intraguild predation may not be as unique a force as is often assumed (Anderson & Semlitsch 2016, Lorda et al. 2016). Rather than directly searching for a competitor, killing it, and feeding on it, an unknown fraction of intraguild predation events are caused by predatory interactions that happen to involve competitors, and competitive killing that leads to opportunistic feeding. This may have implications for the stability of intraguild predation in various systems (Holt & Polis 1997, Roberge et al. 2015, Marroni et al. 2016), and merits further investigation.

It should be noted that while this review offers improved understanding of the broad-scale trends of interspecific killing, it says nothing about the population-level impacts of the behavior, which in a conservation context is of great interest. Interspecific killing has been suggested to limit species predation behaviors and space use (Creel & Creel 2002) and cub mortality rates of threatened species (Laurenson 1994). Because these analyses are performed on the species level, much research remains to be done on the proximate, on-site drivers and consequences of interspecific killing. Particularly, small-bodied carnivorans with limited population size and low connectivity may be more at risk from interspecific killing than previously surmised under the competitive killing framework.

While not true prediction (in that the data used for prediction were also used to fit the model, and so do not constitute an independent training dataset—McGill 2013), the unobserved species interactions with high estimated probabilities in the dataset (Table 5) may help inform future research and associated conservation measures. For example, the killing interactions between pumas and margays (*Leopardus wiedii*) had an 82% predicted chance of observation in the dataset. Margays are listed as Near Threatened by the IUCN, and due to habitat loss and other factors are declining in population size (de Oliveira et al. 2015). Given the margay's relatively low density through its range, and the lack of knowledge of its mortality sources, this interaction may merit further investigation.

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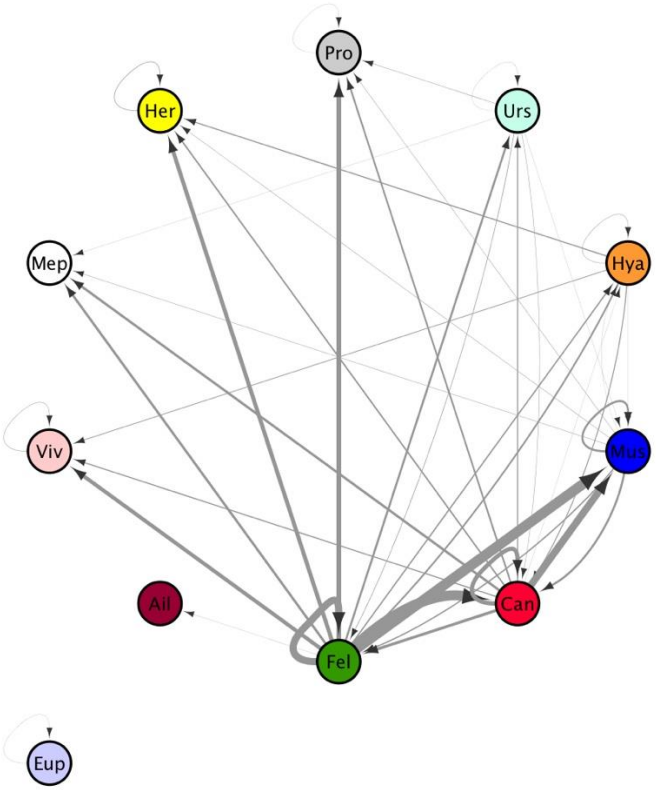

Figure 1: Diagram showing the frequency of killing interactions between and within carnivoran families across datasets. Arrow moves from the killer family to the killed family, and is proportional in width to the number of species interactions reported. Ail = Ailuridae, Can = Canidae, Fel = Felidae, Her = Herpestidae, Hya = Hyaenidae, Mep = Mephtididae, Mus = Mustelidae, Pro = Procyonidae, Viv = Viverridae, Urs = Ursidae.

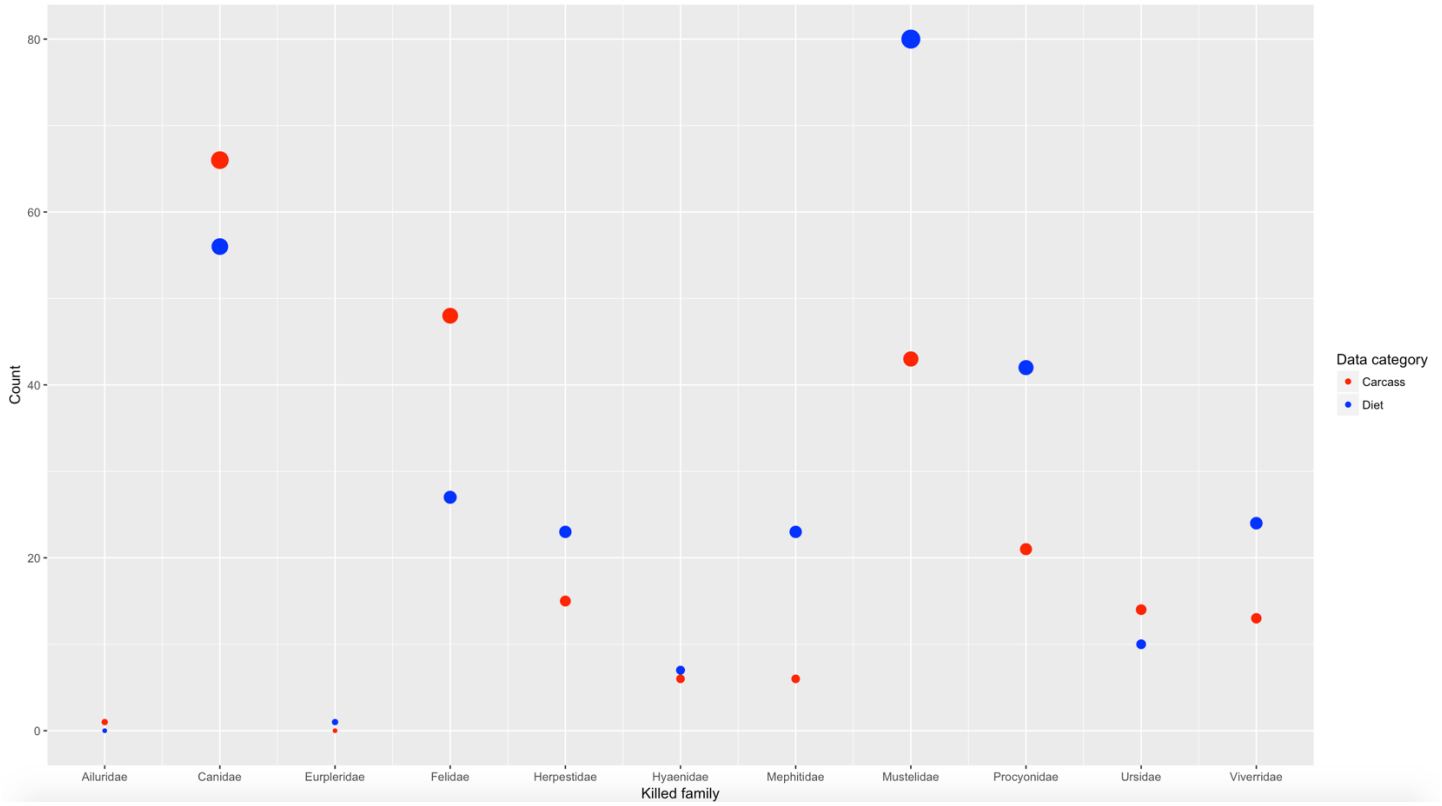

Figure 2: Dotplot showing the number of reported interactions reported for each carnivoran killed family. Dot color denotes the data type (carcass vs. scat or stomach) and dot size is proportional to the number of interactions reported.

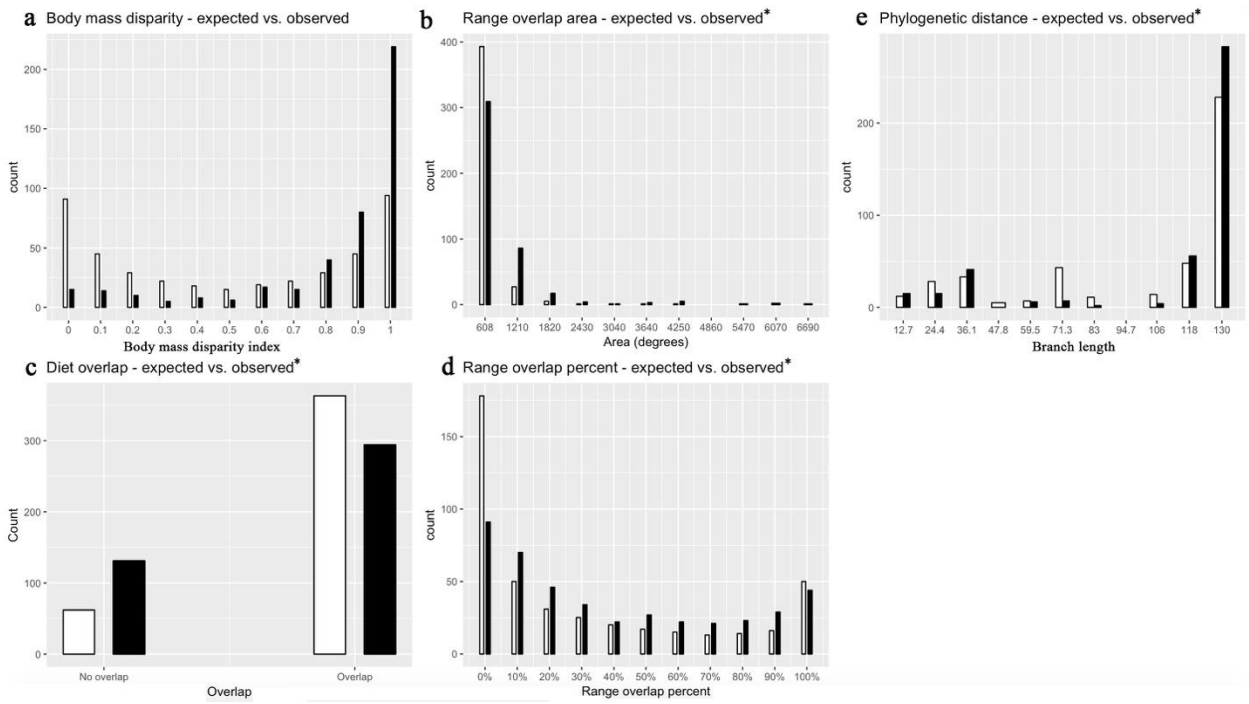

Figure 3: a. Expected (white bars) vs. observed (black bars) scaled body mass disparity index values for the reported species interactions. Numbers above bars denote the ratio between killer species and killed species body masses. b. Expected (white bars) vs. observed (black bars) dietary overlap values for the reported species interactions. c. Expected (white bars) vs. observed (black bars) range overlap values for the reported species interactions. d. Expected (white bars) vs. observed (black bars) phylogenetic distance values between all interacting species. Asterisks (*), denote significant differences between observed and expected distributions at $p < 0.05$.

Figure 4: a. Expected (white bars) vs. observed (black bars) dietary overlap values for the reported species interactions with Felidae killer species. b. Expected (white bars) vs. observed (black bars) dietary overlap values for the reported species interactions with Canidae killer species. Asterisks (*), denote significant differences between observed and expected distributions at $p < 0.05$.

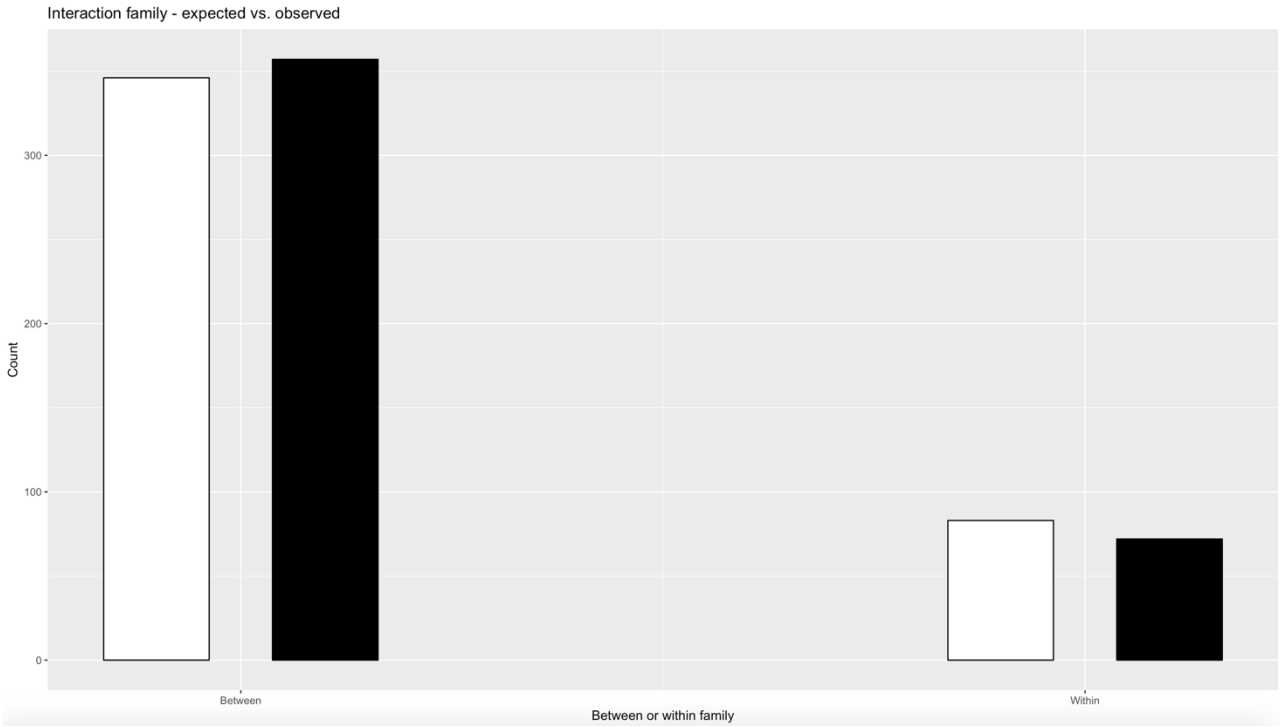

Figure 5: Expected (white bars) vs. observed (black bars) frequency of within family vs. between-family killing relationships in the dataset.

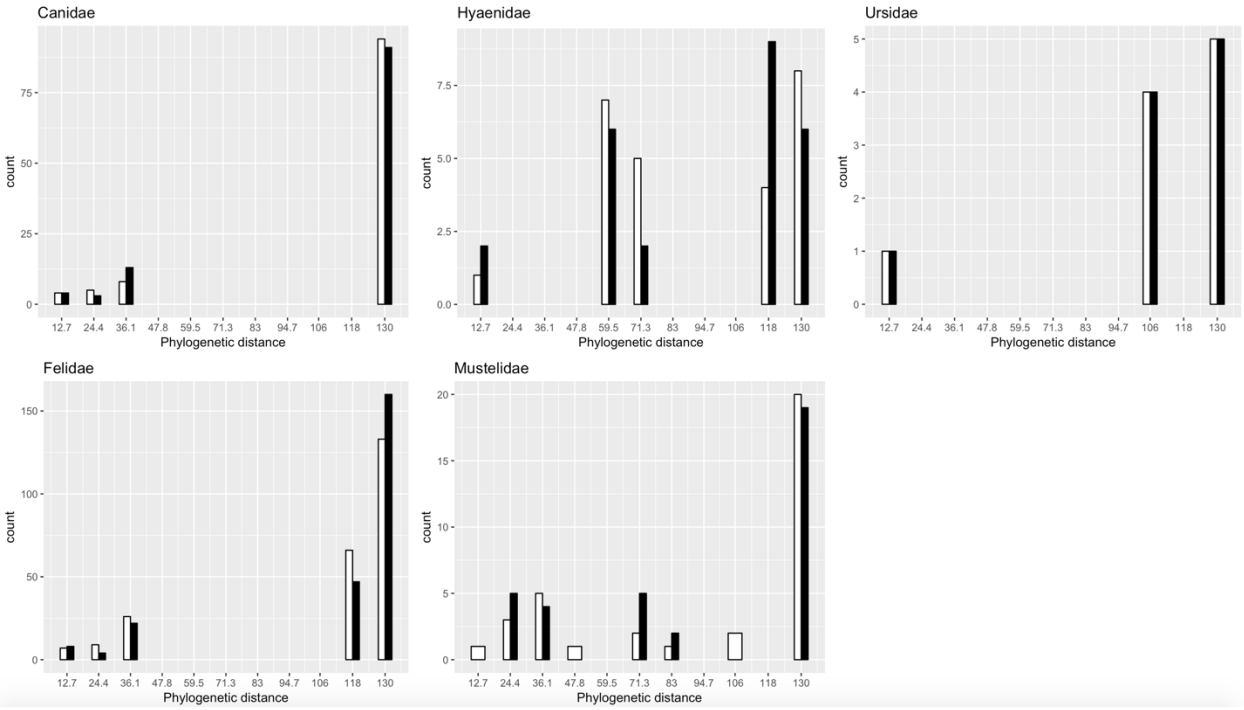

Figure 6: Expected (white bars) vs. observed (black bars) phylogenetic distances for each carnivoran killer family with > 10 observed unique interactions in the dataset.

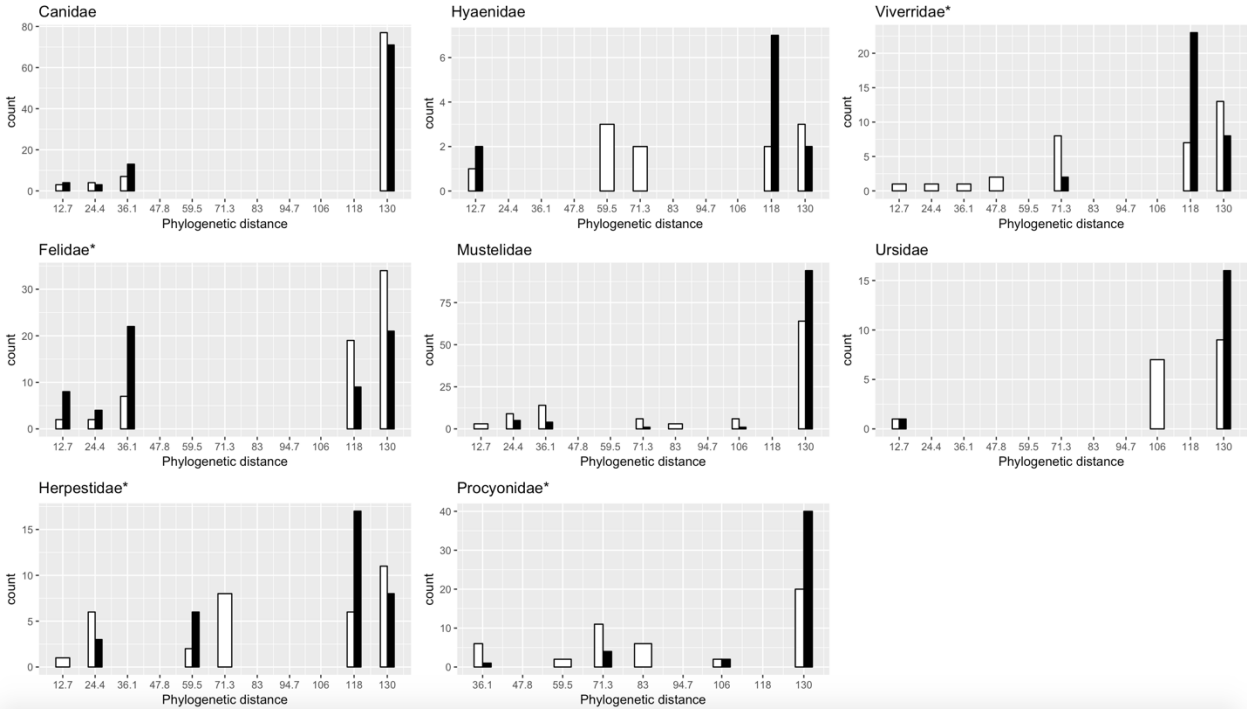

Figure 7: Expected (white bars) vs. observed (black bars) phylogenetic distances for each carnivoran killed family with > 10 observed unique interactions in the dataset. Asterisks (*) denote significant differences between observed and expected distributions at $p < 0.05$.

	Diet overlap	Consume killed species	Body size ratio
Competitive Killing	Y	N	2x-5x*
Predatory Killing	N	Y	No upper limit
Intraguild predation	Y	Y	2x-5x*
Incidental Killing	N	N	No upper limit

Table 1: Summary of key predictions of the four hypotheses evaluated by this paper. The body size ratios marked by asterisks (*) were those proposed by Donadio & Buskirk to be optimal for competition-driven interspecific killing.

Model	**K**	**AICc**	**ΔAICc**	**LL**
KillerS + KilledS	7	2101.68	0	-1043.83
KillerS + KilledF	7	2244.93	143.25	-1115.46
KillerS	6	2254.53	152.85	-1121.26
KillerF + KilledS	7	2309.06	207.38	-1147.52
KillerF + KilledF	7	2508.01	406.33	-1247.00
KillerF	6	2568.71	467.03	-1278.35
KilledS	6	2573.64	471.96	-1280.81
KilledF	6	2747.80	646.12	-1367.90

Table 2: AICc table for each examined combination of model random effects with all fixed effects held constant. KillerS = Killer species. KilledS = Killed species. KillerF = Killer family. KilledF = Killed family.

Model	**K**	**AICc**	**∆AICc**	**LL**
S_BMDI + DietO + Range + PhyDist	7	2101.68	0	-1043.83
S_BMDI + DietO + Range	6	2106.61	4.93	-1047.30
DietO + Range + PhyDist	6	2151.13	49.45	-1069.56
DietO + Range	5	2157.03	55.35	-1073.51
S_BMDI + DietO + PhyDist	6	2181.32	79.64	-1084.66
S_BMDI + Range	5	2183.65	81.97	-1086.82
S_BMDI + Range + PhyDist	6	2193.54	91.86	-1090.77
S_BMDI + DietO	5	2198.32	96.64	-1094.16
Range + PhyDist	5	2231.72	130.04	-1110.86
Range	4	2234.40	132.72	-1113.20
DietO + PhyDist	5	2235.42	133.74	-1112.71
DistO	4	2241.10	139.42	-1116.55
S_BMDI + PhyDist	5	2280.40	178.72	-1135.20
S_BMDI	4	2282.88	181.21	-1137.44
PhyDist	4	2324.84	223.16	-1158.42
(Intercept)	3	2327.60	225.92	-1160.80

Table 3: AICc table for each examined combination of model fixed effects with killer species and killed species as random effects. S_BMDI = Scaled Body Mass Disparity Index. DietO = Dietary overlap. Range = Range overlap. PhyDist = Phylogenetic distance.

M1					
		β	S.E.	z	p
Covariate	(Intercept)	-10	0.92	-14.89	< 0.001
	S_BMDI	3.29	0.5	6.57	< 0.001
	DietO	1.19	0.31	4.1	< 0.001
	Range	0.0012	0.00014	8.9	< 0.001
	PhyDist	0.0025	0.002	1.24	0.215
M2					
		β	S.E.	z	p
Covariate	(Intercept)	-10	0.65	-15.36	< 0.001
	S_BMDI	3.33	0.5	6.64	< 0.001
	DietO	1.13	0.29	3.83	< 0.001
	Range	0.0012	0.00014	8.88	< 0.001

Table 4: Parameter estimates for the best (M1) and second-best (M2) models. See Table 3 for associated AICc scores. S_BMDI = Scaled Body Mass Disparity Index. DietO = Dietary overlap. Range = Range overlap. PhyDist = Phylogenetic distance.

Killer species	**Killed species**	**Probability**
Puma (*Puma concolor*)	Crab-eating fox (*Cerdocyon thous*)	0.84
Black-backed jackal (*Canis mesomelas*)	Wildcat (*Felis silvestris*)	0.82
Puma (*Puma concolor*)	American marten (*Martes americana*)	0.82
Puma (*Puma concolor*)	Margay (*Leopardus wiedii*)	0.82
Wolverine (*Gulo gulo*)	Red fox (*Vulpes vulpes*)	0.82
Lion (*Panthera leo*)	Aardwolf (*Proteles cristata*)	0.82
Coyote (*Canis latrans*)	North American river otter (*Lontra canadensis*)	0.78
Tiger (*Panthera tigris*)	Masked palm civet (*Paguma larvata*)	0.76
Gray wolf (*Canis lupus*)	Northern raccoon (*Proycon lotor*)	0.76
Brown hyena (*Parahyaena brunnea*)	Bat-eared fox (*Otocyon megalotis*)	0.74

Table 5: Species interactions not observed in the interspecific killing dataset with the highest estimated probability of occurrence as predicted by the top models.